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THE MECHANISM OF MOVEMENT AND THE DURATION OF THE EFFECT OF STIMULATION IN THE LEAVES OF DIONAEA[1]

WILLIAM H. BROWN

INTRODUCTION

Charles Darwin (1875) appears to have been the first to investigate the mechanism of leaf closure in Dionaea. He marked the upper surface of the leaf with ink-dots and found that the distances between these decreased slightly as the leaf closed. From this he concluded that closure is due to the active contraction of the upper surface of the leaf. De Candolle, as a result of his morphological studies of Dionaea, advanced the idea that the opening and closing movements of the leaf are due to changes in the turgescence of the parenchyma of the dorsal region. Batalin (1877) concluded that movement is here accompanied by a small amount of actual growth. Munk (1876) expressed the opinion that the closure of the leaves is mainly due to the contraction of the upper surface but added that there is also an expansion of the lower surface. This writer supposed that water passes from the cells of the upper to those of the lower region. Macfarlane (1902) believed that there are structures in the leaves of Dionaea which resemble animal muscles. The prevailing opinion thus seems to have ascribed the closure of Dionaea leaves to the contraction of the dorsal region of the leaf.

The experiments here reported were carried out at the Laboratory of Plant Physiology of the Johns Hopkins University, and the writer is indebted to Prof. B. E. Livingston for valuable assistance in the experimentation and for editorial help in connection with this paper. The plants used were very kindly supplied by Dr. W. D. Hoyt. The fact that much of the literature dealing with plant movements is not available at this Bureau has rendered the above discussion of the literature necessarily very incomplete.

MECHANISM OF STIMULATION MOVEMENTS

The leaves of Dionaea show two distinct types of closing movements. In the first of these, if the leaf is stimulated and the stimulating object is then withdrawn the two lobes approach each other rapidly, the leaf returning to its original condition only after several hours, usually by the following day. When the closure occurs in this way the marginal bristles of the two lobes become interlaced, while the lobes themselves bulge out widely from each other with their ventral surfaces convex. In the second type of movement, when the leaf closes over an insect, the two lobes approach each other in such a way that the ventral surfaces often become concave. This brings the upper surfaces into closer contact with the insect and leaves a smaller opening between the two lobes than is the case with the first type of closure. In the present discussion only the first type of movement will be considered.

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[1] Botanical contribution from the Johns Hopkins University, No. 48.

In order to determine what region of the leaf is most active in causing the closing movement, both the dorsal and ventral surfaces were similarly marked with rows of dots made with India ink and running both parallel to and perpendicular to the midrib. The distances between the dots having been microscopically measured, the leaves were stimulated and the measurements were repeated after closing and again after reopening. In order to measure these distances on the dorsal surface of one lobe, it was necessary to remove part of the opposite lobe, which was accomplished by removing an oblong piece with a sharp scalpel, several days being allowed for the leaf to recover before the beginning of the experiment itself. Such measurements were made on both young and mature leaves of various sizes, but always with similar results.

In Table I. are given the measurements made on the ventral surfaces of five different leaves; the numerals of the experiment numbers refer to the leaf and the letters refer to the successive spaces between dots, from the midrib outward to the margin. The values themselves are merely relative. In the case of No. 1 the leaf was caused to close three successive times and was allowed to reopen after each closure. From these measurements it appears at once that the distances between the transversely arranged dots on the ventral surface increase considerably when the leaf closes and change comparatively little during reopening.

To study the transverse expansion of the lower leaf surface thus indicated as accompanying closure, the percentage of this expansion was calculated for each distance, on the basis of the corresponding measurement obtained when the leaf was in the original open condition. The percentages thus derived are presented, for nine different leaves, in Table II, which includes the data for the leaves referred to in Table I with the corresponding experiment numbers.

TABLE I.

Comparative Measurements of Distances Between Adjacent Dots on the Lower Surface of Dionaea Leaves Before and After the Closing Movement, the Dots Arranged in a Line Transverse to the Midrib

Experiment No.		Leaf Open	Leaf Closed	Leaf Open	Leaf Closed	Leaf Open	Leaf Closed
1	*a*	20.0	22.0	20.0	23.0	23.0	23.0
	b	23.0	23.5	23.5	26.0	27.0	28.0
	c	23.0	29.0	30.0	34.0	34.0	35.0
	d	30.0	34.0	35.0	36.0	36.0	38.0
	e	....	19.0	19.0	20.0	21.0	21.5
2	*a*	21.0	22.0	....	....	....	....
	b	26.0	28.0	....	....	....	....
	c	37.0	40.5	....	....	....	....
	d	25.0	26.5	....	....	....	....
	e	26.0	27.0	....	....	....	....
3	*a*	23.0	23.0	24.0	....	....	....
	b	31.0	32.0	33.0	....	....	....
	c	26.0	29.0	29.0	....	....	....
	d	21.0	22.0	23.0	....	....	....
4	*a*	25.0	27.0	....	....	....	....
	b	17.0	18.0	....	....	....	....
	c	17.0	19.0	....	....	....	....
	d	16.0	17.5	....	....	....	....

From the data of Table II it appears that the lower surface of the leaf lobe expands transversely during the process of closing, the average amount of this expansion for the leaves tested being 6.7 percent of the original distance from the first to the last dot.

The results of similar measurements of the distances between dots placed in rows parallel to the midrib gave similar results, and it thus appears that the area of the whole lower surface increases in extent during closure.

Open leaves are usually slightly curved so that the dorsal surface is somewhat concave and the ventral convex. During the process of closing, with this type of movement, as has been remarked, this curvature becomes much more pronounced. Since the measurements did not give the distances between the dots along the curved surface, but only the rectilinear distances, the amounts of expansion shown in Table I are less than those actually occurring. The distance measured was always the chord of the arc of curvature of the leaf surface.

TABLE II

Percentage of Increase with Leaf Closure, in Distances Between Adjacent Dots on the Lower Surface of Dionaea Leaves, the Dots Arranged in a Line Transverse to the Midrib

Experiment No.	Expansion, 1st Closure	Expansion, 2d Closure	Expansion, 3d Closure
1 *a*	10.0	15.0	0.0
b	2.2	10.6	3.7
c	26.1	13.3	2.9
d	13.3	2.8	5.5
e	....	5.3	2.5
Between extreme dots	13.0	9.0	3.2

Experiment No.	Expansion	Experiment No.	Expansion
	Percent		*Percent*
2 *a*	4.8	3 *a*	0.0
b	7.7	*b*	3.2
c	9.5	*c*	11.5
d	6.0	*d*	4.8
e	3.8		
Between extreme dots	6.7	Between extreme dots	4.9
4 *a*	8.0	5 *a*	12.5
b	5.9	*b*	15.8
c	11.8	*c*	11.6
d	9.4	*d*	10.1
		e	0.0
Between extreme dots	8.7	Between extreme dots	10.0
6 *a*	1.8	7 *a*	3.3
b	4.8	*b*	8.4
c	3.8	*c*	3.7
d	2.6	*d*	1.5
		e	1.2
Between extreme dots	3.3	Between extreme dots	3.9
8 *a*	0.0	9 *a*	3.4
b	30.0	*b*	13.6
c	3.3	*c*	2.8
Between extreme dots	5.7	Between extreme dots	5.7

The results of measurements similar to those just described, made on the upper leaf surface, are given in Table III, which also gives percentages of decrease in the distances between the dots during closing and of increase during opening, as compared to the original distances.

Table III

Comparative Measurements of Distance Between Adjacent Dots on the Upper Surface of Dionaea Leaves Before and After Closing and After Reopening, the Dots Arranged in a Line Transverse to the Midrib, Together with Percentage of Shrinkage During Closure and of Expansion During Reopening

Experiment No.		Distances, Leaf Open	Distances, Leaf Closed	Shrinkage During Closure	Distances, Leaf Reopened	Expansion During Reopening
				Percent		*Percent*
1	*a*	19.0	19.0	0.0	20.0	5.3
	b	20.0	19.7	1.5	22.0	11.7
	c	16.0	15.8	1.3	17.0	7.6
	d	11.0	10.5	4.5	11.5	9.5
Between extreme dots		....	....	1.5	....	9.3
2	*a*	24.0	24.0	0.0	....	....
	b	27.0	26.8	0.7	....	....
	c	20.0	19.7	1.5	....	....
	d	15.0	15.0	0.0	....	....
Between extreme dots		....	....	0.6	....	....
3	*a*	20.0	19.5	2.5	....	....
4	*a*	....	13.5	....	15.0	11.1
	b	....	19.0	....	20.0	5.3
	c	....	25.0	....	27.0	8.0
	d	....	21.0	....	24.0	14.3
Between extreme dots		....	....	....	....	9.6

From the data of Table III it appears that these dots on the upper surface of the leaf approach each other to a slight degree during the closing process. The average decrease thus occurring in the distances between extreme dots of these transverse rows is 1.5 percent of the original distance.

This apparent transverse shrinkage of the upper surface may be explained by the error of measurement just pointed out, due to curvature; the bending of the lobe which accompanies closure should bring the dots on the upper surface closer together without any actual change in the extent of this surface. To test this suggestion, a paper marked with dots at measured distances apart was bent so as to have a form similar to that of a curved leaf lobe, after which the distances between the dots were again measured. In this case the dots approached each other to a greater extent than did those on the dorsal surfaces of the leaves during closure. This seems to indicate that if there is any change in the area of the upper surface during closure it is probably in the direction of an increase rather than in that of a decrease. Although this point is uncertain, it is still quite clear that if any transverse shrinkage occurs in the area of the upper leaf surface this must be practically negligible when compared with the expansion that has been shown for the lower surface. It is thus strongly suggested that the movement of closing is largely due to the increase in volume of tissues lying near the lower leaf surface, although, as will be pointed out later, there appears also to occur a decrease in the turgor of the tissues near the upper surface, which probably also has a contributory effect. This conclusion is contrary to the prevailing opinion in this connection, that leaf closure is due to the contraction of the dorsal tissues.

The reopening of the leaf after it has closed, on the other hand, seems to be due to expansion of the upper layers of cells, for during this process the area of the lower surface changes only slightly while that of the upper enlarges considerably, the measurements here showing an average increase of 9.4 percent.

TABLE IV

Comparative Measurements of Distances Between Adjacent Dots on the Lower Surface of Dionaea Leaves just Before Closing, just After Closing, and 1, 2, and 6 hours After Closing, the Dots Arranged in a Line Transverse to the Midrib

Experiment No.		Just Before Closing	Just After Closing	1 Hour After Closing	2 Hours After Closing	6 Hours After Closing
1	*a*..........	12.0	12.0	12.5	12.5	....
	b..........	5.0	6.5	7.0	6.5	....
	c..........	16.5	17.0	17.0	16.5	....
2	*a*..........	14.5	15.0	15.0	15.0	....
	b..........	11.0	12.5	12.5	12.0	....
	c..........	18.0	18.5	19.0	19.0	....
3	*a*..........	21.0	22.0	22.0	22.5	22.5
	b..........	26.0	28.0	28.0	28.0	28.0
	c..........	37.0	40.5	40.0	40.5	40.5
	d..........	25.0	26.5	26.5	25.5	25.5
	e..........	26.0	27.0	26.5	26.5	26.5

Examination of the data for experiments 1 and 2, given in Table I, indicates that the increase in area of the lower surface during closure is practically permanent and that this enlargement persists after the leaf reopens. That this increase generally remains fairly constant during the period between closing and reopening is shown by the data given in Table IV, in which are recorded the results of hourly measurements made during this period.

The average increase in the distance between the first and last dot on the lower leaf surface, for the entire period of closing and reopening, may be calculated by adding the average percentage increase during closure (6.7 percent) to the average percentage during opening (1.4 percent), the result being 8.1 percent. In the case of the upper leaf surface, the average percentage of shrinkage during closure (1.5 percent) is to be subtracted from the average percentage of expansion during opening (9.4 percent) leaving 7.9 percent as the total percentage of increase in the transverse direction for the upper surface. These two values are very nearly alike and their average, which is 8.0 percent, may be taken to represent the transverse enlargement of the lobe during the entire period of closing and reopening.

It is worthy of note that the average transverse shrinkage of the upper surface during closure (1.5 percent) is nearly equal to the average expansion of the lower surface during opening (1.4 percent). As has been seen, the former of these apparent changes is probably to be explained as due to an error in measurement, resulting from the curvature of the leaf lobe when closed, and it seems equally probable that the measurement of the lower surface during opening is subject to a similar error, but of opposite direction resulting from the straightening of the leaf lobe, which makes the dots appear farther apart in rectilinear distance. It is therefore not unlikely that all of the apparent expansion of the lower surface during opening is attributable to this error.

It remains to enquire whether the rate of transverse enlargement of these leaf lobes is greater during the period of closing and opening than at other times. As shown above, this enlargement amounts to about 8.0 percent. To answer this question three leaves of different ages were selected and one lobe of each was marked on the lower surface, with a row of ink dots reaching from the midrib to the margin as in the previous cases, the distances between the dots being then measured at intervals of from 1 to 8 days. The results of these measurements are given in Table V.

The last column of Table V presents the total amount of enlargement for the entire period of observation, on the basis of the original measurements. The first of the experiments here referred to continued 18 days, and the total transverse enlargement, from the first to the last dot, was only 3.1 percent for this entire period, which is much less than the enlargement in the same direction shown by the lower surface of stimulated leaves for the much shorter period of closing and reopening. The second experiment lasted seven days and the total expansion recorded was 1.4 percent. The third experiment also continued seven days, but showed a greater amount of total enlargement than did either of the other two, this being 9.6 percent. If the percentage of total transverse enlargement of the ventral surface of the leaf lobe be divided by the number of days in each case, the average daily rates for the three cases prove to be: 0.17, 0.20, and 1.36 percent, respectively. The highest of these average daily rates is only 43.7 percent of the smallest corresponding total enlargement recorded for the period of closing and opening in the case of stimulated leaves. The average daily rate of increase in the distance between the extreme dots on the lower surface in the case of unstimulated leaves

TABLE V

Comparative Measurements of Distances Between Adjacent Dots on the Lower Surface of Unstimulated Dionaea Leaves, the Dots Arranged in a Line Transverse to the Midrib, to Show Rates of Transverse Enlargement

Experiment No.		At Beginning of Experiment	After 1 Day	After 2 Days	After 3 Days	After 4 Days	After 6 Days	After 7 Days	After 8 Days	After 10 Days	After 18 Days	Total Enlargement
												Percent
1	*a*	22.0	22.0	23.0	23.0	....	22.0	....	22.0	22.0	22.0	0.0
	b	25.0	25.0	25.0	26.0	....	26.0	....	26.0	26.0	26.0	4.0
	c	30.5	30.5	30.0	30.5	....	31.0	....	31.0	31.0	31.5	3.3
	d	33.0	33.5	33.3	33.0	....	33.0	....	33.0	33.0	34.5	4.5
	e	18.0	18.0	18.0	18.0	....	18.5	....	18.0	18.0	18.5	2.8
Between extreme dots		......	....	....	....	....	....	....	....	....	....	3.1
2	*a*	27.0	....	27.0	....	27.0	....	27.0	....	....	....	0.0
	b	33.5	....	33.5	....	34.0	....	34.0	....	....	....	1.5
	c	26.0	....	26.0	....	27.0	....	27.0	....	....	....	3.9
	d	19.0	....	19.0	....	19.0	....	19.0	....	....	....	0.0
Between extreme dots		......	....	....	....	....	....	....	....	....	....	1.4
3	*a*	13.5	....	13.5	....	15.0	....	15.0	....	....	....	11.1
	b	19.0	....	19.0	....	20.0	....	20.0	....	....	....	5.2
	c	25.0	....	25.0	....	26.5	....	27.0	....	....	....	8.0
	d	21.0	....	21.0	....	23.0	....	24.0	....	....	....	14.3
Between extreme dots		......	....	....	....	....	....	....	....	....	....	9.6

is 0.58 percent, while the average corresponding enlargement in the case of stimulated leaves, during closure alone is 6.73 percent. Thus, the transverse expansion of the ventral surface during closure of stimulated leaves is 11.6 times as great as is the average daily rate of transverse enlargement shown by the lower surfaces of unstimulated leaves. From these figures it is evident that the stimulation movements are accompanied by a greatly accelerated rate of transverse enlargment.

Accelerated activity is, in general, accompanied by depletion of previously accumulated material, by increased formation of the products of cell activity, and sometimes even by the formation of products not otherwise produced. It is therefore suggested that, if closure of these Dionaea leaves is accompanied by accelerated growth, the response should be less vigorous after successive closures, and the results of experiment 1, as shown in Tables I and II, are in agreement with this suggestion. In this experiment the distance between the first and last dot increased 13.0 percent during the first closure, 9.0 percent during the second, and only 3.2 percent during the third response. Moreover, after this last closure the leaf opened very slowly and the process required a number of days, the extreme slowness of the opening movement rendering it practically impossible to decide just when the opening was complete. Also, it has been generally found in this study that plants become sickly and die when the leaves are repeatedly stimulated at short intervals.

The idea is at once suggested that we are here dealing with something closely related to the condition of fatigue, which has been clearly demonstrated for certain other motile responses in plants. For example, the stigma lobes of *Martynia* (Brown, 1913) respond to contact stimulation by a rapid drawing together, which is followed by a return to the usual position, the latter process requiring from 8 to 40 minutes. If these stigmas are repeatedly stimulated, each new stimulus being applied as soon as the lobes have regained their usual position, the period required for opening may become shorter after the first and second response, but it then becomes longer and longer as stimulation is repeated, until the stigmas at length fail to respond to contact stimulation at all. Here it is not clear whether the decrease in rate of movement is due to an accumulation of toxic substances, as in the case of animal muscle, or to the using up of available material, but the latter supposition seems to be the more probable of the two.

In the case of Dionaea it also appears probable that the decreased activity observed with repeated stimulation may be due to depletion of previously accumulated materials, for considerable material must be expended in the excessive growth that follows stimulation. Such an enlargement might occur on account of either one of three possible causes, or on account of two or more acting together. (1) A sudden increase in the osmotic pressure of the cells that expand might stretch the cell walls and lead to permanent enlargement, without any preliminary change in the walls themselves. (2) The osmotic pressure of the cells in question might remain the same, but the extensibility of their cell walls might be increased (or their tendency to contract decreased) so that the same pressure as was previously effective only to hold them in equilibrium might now produce enlargement. This hypothesis seems very improbable. (3) Finally, the osmotic attraction for water exerted by the cells near the upper surface might be decreased, so as to allow water to pass from these cells into those near the lower surface, thus allowing an expansion of the latter due to their original osmotic pressure. In any of these three cases the enlargement of the tissues on the lower side of the lobe must be concomitant with the passage of water into these cells due to their osmotic activity.

Evidence will be adduced below showing that stimulation is followed by a decrease in the osmotic pressure of the cells of the upper layers, which would allow the passage of water out of these cells into those of the lower region, but it seems hardly probable that sufficient water to cause the observed changes may thus enter the lower cells unless one of the other possibilities just mentioned also becomes effective; it is to be supposed that these lower cells have attained equilibrium, as far as water is concerned, under the previously existing conditions of their osmotic pressure and of the elasticity of their walls. If the closing movement of Dionaea leaves occurred only at times of the day when incipient drying of the lower leaf tissues [Livingston and Brown (1912)] might be postulated, then the enlargement of these cells might occur because of the release of a large amount of water from the cells of the opposite side, but these leaves are capable of vigorous movement at all hours of the day, so that this supposition cannot be upheld.

If the closing movement were due to a stretching of the cell walls of the lower region, later rendered permanent by growth, then leaves killed just after closure might perhaps be made to reopen by replacing the water in the cells by some liquid in which their osmotically active solutes were insoluble. By thus precipitating these solutes the osmotic pressure of the cells would be removed and the leaves might resume their original form. Returning such leaves to water should then cause them to close again, providing the protoplasmic membranes had not been too greatly altered and providing the re-entering water might replace the other liquid and again bring the solutes into aqueous solution. In such a case the original osmotic pressure would be restored to all cells and those of the ventral region should again become stretched as at first. To test this possibility a number of leaves (some open, some just closed by stimulation, and some closed for a half-hour or longer) were killed in boiling water and then passed through alcohol to xylene. Since sugars are practically insoluble in xylene, the replacement of the water of the cells by this liquid should result in a precipitation of sugars, which may be supposed to be of prime importance in producing the usual osmotic pressure. The leaves killed just after closure reopened in xylene, while those that were open and those that had been closed for some time when killed showed no alteration. All of the leaves were then returned through alcohol to water, which resulted in re-closure of those that had opened in xylene, while the others still remained unaltered. In some cases such transfers from water to xylene and back again were repeated a number of times with the same leaf, and the results were always like those just described. As might be expected the distances between adjacent ink-dots on the lower surfaces of leaves, showing movement decreased when the leaves were changed from water to xylene and increased when the reverse transfer was made. The comparative measurements from such a transfer of a leaf killed just after closing, from water to xylene and back to water, are given in Table VI.

TABLE VI

Comparative Measurements of Distances Between Adjacent Dots on the Lower Surface of Dionaea Leaves Killed Just After Closing, as the Leaves were Transferred From Water Through Alcohol to Xylene and Back to Water, the Dots Arranged in a Line Transverse to the Midrib

Experiment No.	Leaf in Water	Leaf in Alcohol	Leaf in Xylene	Leaf in Alcohol	Leaf in Water
I *a*..........	42	42	37	42	42
b..........	28	27	26	27	28
c..........	52	50	46	50	52

It appears that the only way by which transfer from water to xylene may produce opening of the leaf, as above described, must be through the removal of the osmotic pressure in all of the cells, and these experiments seem to show that the stimulation closure that had occurred just before the experiment began was due to a stretching, by osmotic pressure from within, of the cell walls of the ventral portion of the leaf. It thus appears that the movement of closure is due to stretching of these cell walls rather than by ordinary growth. The enlargement thus effected is soon fixed by permanent growth changes, however, as is shown by the fact that the transfer from water to xylene does not affect the form of the leaves if these have been closed for a half-hour before being killed. Since the tests involving measurements of the changes in the surface dimensions of normal leaves as these close and reopen agree with the experiment just described, it seems clear that stimulation closure is not due to an active contraction of the tissues near the dorsal surface, but is due to osmotic expansion of the cells in the ventral region.

The supposition that the closing response in Dionaea leaves may be due to alterations in the permeability of the protoplasmic membranes seems to be excluded by the experiments described above. Enlargement of the cells in the ventral region must be preceded and accompanied by entrance of water into these cells, probably from those of the dorsal region. Changes in permeability might account for the passage of water out of the latter cells although as Pfeffer (1906) points out this would necessitate the movement of dissolved substances along with the water. Changes in permeability can not, however, explain the passage of water into the cells of the ventral region of the leaf, and it is this movement of water which appears to be the first condition necessary for stimulation closure.

A study of the cell contents in stimulated and unstimulated leaves of Dionaea brought out some interesting and apparently important facts. Forty-eight apparently normal and sensitive leaves were killed in boiling water, some open, others just after closing and still others fifteen minutes or more after closing, and all were then examined for starch. Those killed while open showed very little or no starch in any of their cells, but when starch occurred most of it was in the upper epidermis and all of it was in the upper region of the leaf, between the veins and the dorsal surface. Leaves killed just after closing gave similar results. Those that had been closed for fifteen minutes or more at the time of killing showed all of the cells between the veins and the dorsal surface packed with starch, while the cells between the veins and the ventral surface contained no starch. The formation of starch thus indicated can not be considered as responsible for closure, since it did not occur until after the leaf had been closed for some time, but this starch formation may have been connected in some way with the same conditions as those that led to closure.

According to Pfeffer (1900, p. 326), Böhm was able to produce a deposition of starch by plasmolyzing cells with potassium nitrate solution. This suggests that the formation of starch occurring soon after closure in the cells of the dorsal region of Dionaea leaves may be caused by a pronounced extraction of water from these cells, such an extraction being brought about through a greatly increased absorptive power of the cells of the ventral region. It seems unlikely, however, that the osmotic concentration of the solution in the latter cells may become great enough to withdraw water from the cells of the dorsal region in sufficient amount to bring about the deposition of starch in the quantities observed.

It seems more probable that the sugar in the cells of the dorsal region of the leaf becomes less active osmotically as a response to stimulation, perhaps by being changed into some substance intermediate between sugar and starch, and if this occurs it should allow a movement of water out of these cells into the cells of the ventral region. Whether or not this sort of removal of sugar from solution in the dorsal cells does actually occur as a concomitant of leaf closure, it appears highly probable that there occurs, with stimulation, an increase in the osmotic attraction for water in the cell sap of the ventral cells. As has been mentioned above, it seems improbable that a sufficient amount of water to cause the observed stretching may pass into the cells of the ventral region unless this movement is preceded by an increase in the osmotic attraction for water exerted by the latter cells. That the causal change may be an alteration in the cell walls of the ventral region appears highly improbable, as has been noted.

In connection with the changes in the starch content of the tissues of these leaves, it may be mentioned that leaves that failed to respond to stimulation showed peculiarities in their starch content. There appeared to be two classes of leaves that did not respond to stimulation in these studies. Those of the first class were exceptionally thick and the lobes were usually slightly reflexed. While in this condition, which did not appear to be connected with their age, they did not respond to mechanical stimulation but they became sensitive later. During the apparently insensitive phase all of the cells contained considerable starch. Leaves of the second class were exceptionally thin, never contained starch either before or after stimulation and never showed any response. Such leaves were characteristic of certain plants, and were not observed to alter in the respects mentioned as they became older. The large amount of starch found in the first class of insensitive leaves, suggesting high osmotic pressure of their cells, and the entire absence of starch in leaves of the other class may perhaps be connected with the failure of these leaves to respond to mechanical stimulation.

The curvature of the primary pulvini of Mimosa, according to Pfeffer (1906), while aided by the force of gravitation acting upon the leaf segments, is mainly produced by an active contraction of the cell walls of the lower region and by compression exerted by the cells of the upper region, the latter remaining turgid after stimulation while the lower cells become flaccid. This flaccidity is brought about by loss of turgor due to the passage of water out of the cells into the intercellular spaces of the shrinking region of the pulvinus. Brown (1912) has shown that curvature may be produced in killed pulvini of Mimosa leaflets, as in the leaves of Dionaea, by transferring them from water through alcohol to xylene. In Mimosa, however, no movement is produced if the curvature has been completed before the pulvini are killed. If curvature has not been completed at the time of killing, transfer to xylene results in the completion of the curvature, and a return from xylene to water causes these leaflets to resume the position which they had when killed. Transfer from water to xylene must reduce the osmotic pressure in all the cells of the pulvini, and the movement of the dead organs seems, therefore, to have been due to shrinkage of the cells of the concave region while those of the convex region remained more rigid.

These experiments appear to be in agreement with Pfeffer's results, and they emphasize an apparent difference between Mimosa and Dionaea. In Dionaea, only leaves killed just after closing show opening movement when transferred from water to xylene; such leaves open by reason of decreased osmotic pressure in the cells of the convex region, this pressure having previously served to keep the tissue of this region in a stretched condition. Closing movement in Mimosa appears to be due largely to a contraction of the cells of the concave region, while closing movement in Dionaea is due largely to an expansion of the cells of the convex half. In Dionaea there is probably also an outward passage of water from the cells of the concave region, as in Mimosa, but in Dionaea this water appears to pass into the cells of the concave region instead of into intercellular spaces. Another case in point is the rapid contraction movement of the stamens of the Cynareae, due, according to Pfeffer (1906), to passage of water from cells to intercellular spaces, as in Mimosa.

Superficially, the mechanism of movement in Dionaea resembles more closely that exhibited by tendrils than it does the mechanism of the movement just mentioned. Fitting (1903) observed that curvature in tendrils is due to change in the rates of growth on the opposite sides of the organ. According to this writer there is here, as in Dionaea, a pronounced temporary acceleration of the growth of the convex half, while, also as in Dionaea, the average rate of growth is also increased. After a temporary stimulation the tendril straightens and at the same time ceases to elongate. The opening of Dionaea leaves is also due to an increased rate of growth on the concave side.

The geotropic and heliotropic curvatures of growing organs are also due to unequal rates of growth on the opposite sides (Pfeffer, 1906). In this case growth is increased on the convex side but, according to the measurements of Sachs, there is a retardation of the average rate. If, as seems likely, there is a decrease in osmotic pressure in the concave region of Dionaea leaves and an increase of pressure in the opposed region, this feature of the movement in Dionaea is similar to the geotropic movements of pulvini that have ceased growing. According to Pfeffer (1906) Hilliard found, by plasmolysis, that geotropic curvature in such organs is accompanied by a decrease in osmotic pressure on the concave side and an increase on the convex side. If, on the other hand, the increase in the dimensions of the convex side of the leaf of Dionaea is connected with an increased extensibility of the cell walls, this is similar to the stretching of the convex side of growing organs showing geotropic and heliotropic curvatures, where the stretching is soon fixed by growth.

It thus seems that the phenomena connected with the mechanism of movement in Dionaea leaves are, except for the rate at which movement occurs, very similar to those shown in geotropic and heliotropic curvatures, and that there is as great a similarity between these two types of movement as there is between those shown by Dionaea and by Mimosa. The movement in Dionaea may perhaps be considered as intermediate in character between such movements as are exhibited in geotropic and heliotropic curvatures, on the one hand, and the rapid movement resulting from mechanical stimulation in Mimosa on the other.

Duration of the Effect of Stimulation

Macfarlane (1902) states that at least two mechanical stimuli are necessary to produce closure of Dionaea leaves and that the number of stimuli required increases as the time period between successive stimuli is lengthened. Brown and Sharp (1910) found that at temperatures around 2° C. two stimuli are usually necessary for closure, but that at 35° C. a single stimulus is frequently sufficient. These writers state that if stimuli are applied at intervals of from 20 seconds to 3 minutes the number of these necessary to produce closure increases with the time elapsing between the application of the stimuli. They also showed that if one of the sensitive bristles on the inner surface of the leaf of Dionaea is stimulated by more than a very slight touch, the effect is independent of the amount of bending of the bristle, each such stimulus, regardless of its intensity, producing the maximum effect for a stimulus of that kind. It is therefore easy to apply several successive stimuli at equal time intervals, and to repeat such a series with different time intervals, the intensity of the force applied to the sensitive bristle requiring no serious attention in this case. The present section deals with the results of a study carried out in the way just suggested.

In each experiment a series of mechanical stimuli were applied to a single sensitive bristle, at equal intervals of time, and record was made of the number of stimuli required to produce the first visible response, and of the number required to produce complete closure of the leaf. In different experiments the length of the equal time intervals ranged from 20 seconds to 20 minutes. All these experiments were carried out with a temperature of about 21° C. On account of the general importance of this sort of data in the physiology of response, and because of the tediousness of such experiments, the results of these series are presented in full in Table VII. They are summarized by averages in Table VIII.

TABLE VII

Response of Dionaea Leaves to Repeated Contact Stimuli, With Various Lengths of Time Intervening Between the Stimuli

Time Period Between Stimuli	Experiment No.	No. of Stimuli Before Complete Closure	Time Between First Stimulus and Complete Closure	No. of Stimuli Before Beginning of Movement	Time Between First Stimulus and Beginning of Movement	No. of Stimuli Between Beginning of Movement and Complete Closure	Time Between Beginning of Movement and Complete Closure
min.			*min.*		*min.*		*min.*
0.33	1	2	0.33	2	0.33	....	....
	2	2	0.33	2	0.33	....	....
	3	2	0.33	2	0.33	....	....
	4	2	0.33	2	0.33	....	....
	5	2	0.33	2	0.33	....	....
	6	2	0.33	2	0.33	....	....
	7	2	0.33	2	0.33	....	....
	8	2	0.33	2	0.33	....	....
	9	2	0.33	2	0.33	....	....
	10	2	0.33	2	0.33	....	....
	Average	2	0.33	2	0.33	....	....
0.67	1	2	0.66	2	0.66	....	....
	2	2	0.66	2	0.66	....	....
	3	2	0.66	2	0.66	....	....
	4	2	0.66	2	0.66	....	....
	5	2	0.66	2	0.66	....	....
	6	2	0.66	2	0.66	....	....
	7	3	1.33	2	0.66	1	0.66
	8	3	1.33	2	0.66	1	0.66
	9	3	1.33	2	0.66	1	0.66
	10	3	1.33	2	0.66	1	0.66
	11	4	2.66	4	2.66	....	....
	12	5	3.33	3	2.00	2	1.33
	Average	2.75	1.27	2.25	0.94	0.50	0.33
1	1	3	2	2	1	1	1
	2	3	2	2	1	1	1
	3	3	2	2	1	1	1
	4	3	2	2	1	1	1
	5	4	3	3	2	1	1
	6	4	3	3	2	1	1
	7	4	3	3	2	1	1
	8	5	4	4	3	1	1
	9	5	4	4	3	1	1
	Average	3.77	2.77	2.77	1.77	1.00	1.00
2	1	5	6	4	6	1	2
	2	6	10	5	8	1	2
	3	6	10	5	8	1	2
	4	6	10	5	8	1	2
	5	6	10	5	8	1	2
	6	7	12	5	8	2	4
	7	7	12	6	10	1	2
	8	7	12	6	10	1	2
	9	7	12	6	10	1	2
	Average	6.33	10.66	5.22	8.44	1.11	2.22

TABLE VII—*Continued*

Time Period Between Stimuli	Experiment No.	No. of Stimuli Before Complete Closure	Time Between First Stimulus and Complete Closure	No. of Stimuli Before Beginning of Movement	Time Between First Stimulus and Beginning of Movement	No. of Stimuli Between Beginning of Movement and Complete Closure	Time Between Beginning of Movement and Complete Closure
min.			*min.*		*min.*		*min.*
3	1	5	12	4	9	1	3
	2	5	12	4	9	1	3
	3	8	21	4	9	4	12
	4	8	21	6	15	2	6
	5	9	24	7	18	2	6
	6	9	24	8	21	1	3
	Average	7.33	19.0	5.50	13.50	1.83	5.50
4	1	6	20	4	12	2	8
	2	8	28	7	24	1	4
	3	9	32	7	24	2	8
	4	9	32	7	24	2	8
	5	9	32	7	24	2	8
	6	9	32	7	24	2	8
	Average	8.33	29.33	6.50	22	1.83	7.33
5	1	7	30	5	20	2	10
	2	7	30	5	20	2	10
	3	7	30	5	20	2	10
	4	7	30	5	20	2	10
	5	8	35	6	25	2	10
	6	10	45	6	25	4	20
	7	12	55	6	25	6	30
	8	12	55	6	25	6	30
	Average	8.75	38.75	5.50	22.50	3.25	16.25
7	1	6	35	5	28	1	7
	2	9	56	7	42	2	14
	3	9	56	7	42	2	14
	4	11	70	8	49	3	21
	5	12	77	9	56	3	21
	6	16	105	10	63	6	42
	Average	10.50	66.50	7.66	46.66	2.83	19.83
10	1	6	50	5	40	1	10
	2	12	110	8	70	4	40
	3	12	110	9	80	3	30
	4	12	110	9	80	3	30
	5	13	120	10	90	3	30
	6	15	140	12	110	3	30
	7	15	140	12	110	3	30
	8	16	150	15	140	1	10
	Average	12.62	116.25	10.00	90.00	2.62	26.25

TABLE VII—*Continued*

Time Period Between Stimuli	Experiment No.	No. of Stimuli Before Complete Closure	Time Between First Stimulus and Complete Closure	No. of Stimuli Before Beginning of Movement	Time Between First Stimulus and Beginning of Movement	No. of Stimuli Between Beginning of Movement and Complete Closure	Time Between Beginning of Movement and Complete Closure
min.			*min.*		*min.*		*min.*
15	1	10	135	8	105	2	30
	2	11	150	8	105	3	45
	3	13	180	8	105	5	75
	4	15	210	10	135	5	75
	5	16	225	8	105	8	120
	6	16	225	8	105	8	120
	7	16	225	10	135	6	90
	8	17	240	11	150	6	90
	9	20	285	9	120	11	165
	10	22	315	14	195	8	120
	Average	15.60	219.00	9.40	126.00	6.20	93.00
20	1	14	260	12	220	2	40
	2	16	300	13	240	3	60
	3	16	300	13	240	3	60
	4	18	340	13	240	5	100
	5	19	360	13	240	6	120
	6	19	360	15	280	4	80
	7	20	380	14	260	6	120
	8	20	380	19	360	1	20
	9	23	440	17	220	6	120
	10	26	500	15	280	11	220
	Average	19.10	362.00	14.40	268.00	4.70	94.00

TABLE VIII

Response of Dionaea Leaves to Repeated Contact Stimuli, With Various Lengths of Time Intervening Between the Stimuli, Being a Summary of the Averages from Table VII

Time Period Between Stimuli	No. of Stimuli Before Complete Closure	Time Between First Stimulus and Complete Closure	No. of Stimuli Before Beginning of Movement	Time Between First Stimulus and Beginning of Movement	No. of Stimuli Between Beginning of Movement and Complete Closure	Time Between Beginning of Movement and Complete Closure
min.		*min.*		*min.*		*min.*
0.33	2.00	0.33	2.00	0.33	0.00	0.00
0.66	2.75	1.27	2.25	0.94	0.50	0.33
1	3.77	2.77	2.77	1.71	1.00	1.00
2	6.33	10.66	5.22	8.44	1.11	2.22
3	7.33	19.00	5.50	13.50	1.83	5.50
4	8.33	29.33	6.50	22.00	1.82	7.33
5	8.75	38.75	5.50	22.50	3.25	16.25
7	10.50	66.50	7.66	46.66	2.83	19.83
10	12.62	111.25	10.00	90.00	2.62	26.25
15	15.60	219.00	9.40	126.00	6.20	93.00
20	19.10	362.00	14.40	268.00	4.70	94.00

From a study of these tables it is seen that if two stimuli are applied with an interval of 20 seconds (0.33 min.) between them, closure occurs immediately after the latter stimulus, taking only a few seconds. When the interval between the two stimuli is forty seconds (0.67 min.) there may be only a partial closure following the latter stimulus. As the interval between the stimuli becomes greater the number of stimuli required for closure increases, as do also the number of stimuli necessary before a visible effect is produced, and the number between the first partial closure and complete closure. When the intervals are very long closure is so gradual as to be quite imperceptible; nevertheless the lobes slowly approach each other and complete closure is finally attained, even with intervals of 20 minutes, which were the longest intervals employed. In one case 26 stimuli were applied, the total period of time between the occurrence of the first stimulus and complete closure being 8 hours and 20 minutes. In this experiment three hours and 40 minutes elapsed between the occurrence of the first visible change and the attainment of complete closure. Between this slow movement and the ordinary rapid closure there is a gradual intergradation as is shown by the data of Tables VII and VIII.

Here also there is an apparent similarity between the phenomena of leaf closure in Dionaea and those of geotropic curvature; in the latter case the reaction time may also be lengthened or shortened. Thus Czapek (1895) has shown that by subjecting the roots of *Vicia faba* to varying amounts of centrifugal force the reaction may take place in from three fourths of an hour to 8 hours. Fitting (1905) has investigated the summation of geotropic stimuli of short duration and has found that single short stimuli are not sufficient to produce curvature but that curvature takes place even though the lengths of the individual stimuli are greatly shortened, provided only that the length of time between the stimuli is not too great. Brown and Sharp (1910) have shown that in the case of Dionaea there may be a summation of individual mechanical or electrical stimuli of low intensities. In one case, when feeble electrical stimuli were applied at intervals of 15 seconds, movement did not occur until after the twenty-eighth stimulus.

The relation between the number of stimuli necessary for the closure of Dionaea leaves and the length of the time interval between the consecutive stimuli is shown graphically in figure 1, in which the ordinates represent the time intervals between the successive stimuli and the abscissas denote the average number of stimuli required to produce closure.

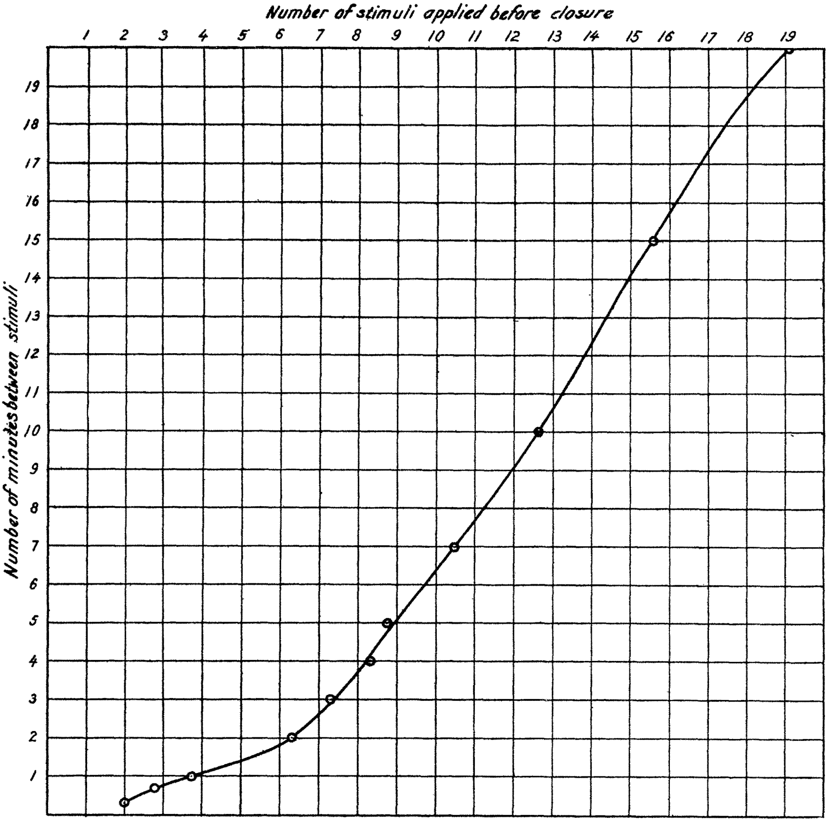

FIG. 1. Graph showing relation between the number of successive stimuli necessary for the closure of the leaf of Dionaea, and the time interval separating the individual stimuli; data from Table VIII.

This graph shows at once that the number of stimuli required for complete closure of the leaf is not proportional to the length of time intervening between the successive stimuli, excepting with time intervals of from 2 to 4 minutes; this portion of the curve, and this portion only, has a slope of approximately 45°. With time intervals of from 20 seconds to 2 minutes the curve is less steep (or more nearly horizontal) and with intervals longer than 3 minutes it is somewhat steeper (more nearly vertical). The curve is thus roughly divided into two portions, the upper of which is steeper than the lower. This main bend in the curve may be of considerable importance, but the physiological conditions determining it appear to be as yet quite unknown.

SUMMARY

The closure of Dionaea leaves is due largely to an increase in the size of the cells of the ventral or convex region, this increase being due to stretching of the cell walls, which soon becomes fixed by growth.

The opening of the leaf is due to slow enlargement, by growth, of the cells of the dorsal or concave region.

Stimulation of the leaf results in a greatly accelerated rate of growth.

Stimulation appears to be immediately followed by a decrease in the osmotic pressure of the cells of the dorsal region, resulting in a passage of water from these cells to those of the ventral region.

A large quantity of starch is deposited in the cells of the dorsal region soon after closure occurs.

Leaves that have been killed in boiling water just after closure, open if transferred through alcohol to xylene and close again when replaced in water.

The mechanism of movement in Dionaea leaves shows many points of apparent similarity to that of geotropic curvatures.

At 21° C. two mechanical stimuli are usually necessary to produce closure in these leaves, but if the time interval between the successive stimuli is increased the number of stimuli necessary for closure also increases, though the latter increase is not proportional to the total time period involved in the reaction.

In one case when stimuli were applied at 20-minute intervals, closure was not complete until eight hours and twenty minutes after the application of the first stimulus.

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MANILA, P. I.

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